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POSITION OF SCUTELLUM AND HOMOLOGY OF COLEOPTILE IN MAIZE

(WITH ELEVEN FIGURES)

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The homologies of the grass embryo and their bearing upon ideas of the phylogenetic relationship of monocotyledonous and dicotyledonous plants have been subjects of study and discussion for a long time, and although most botanists are fairly well agreed upon most phases of the question, some points are still subject to controversy. It is realized that evidences drawn from a single species as highly specialized as maize will not go far toward the making or the breaking of a theory, but two things have been observed in the structure and development of the embryo of *Zea Mays* that seem to have a definite bearing upon the subject, and these are offered for what they may be worth.

The history of the subject has been fully reviewed, and certain sharply contrasted opinions have been presented recently by WORSDELL and by COULTER and LAND. Further reference to the voluminous literature seems unnecessary here, and only those points to which the information at hand is related will be considered.

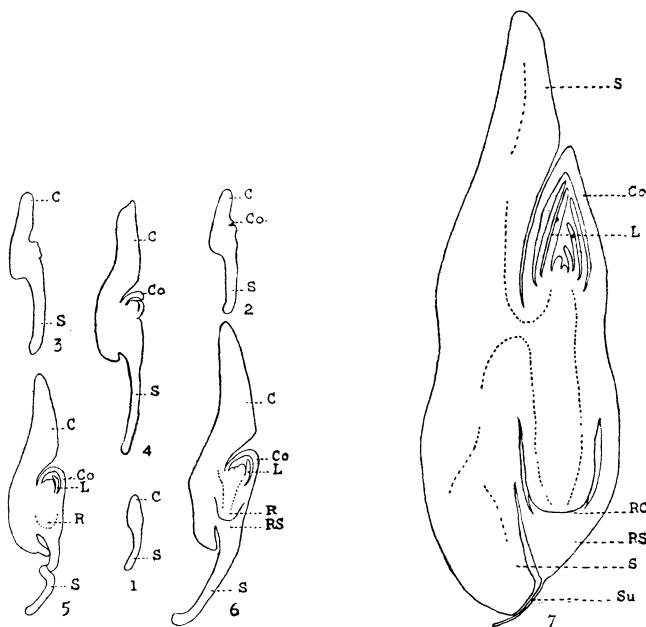
COULTER and LAND¹ maintain that the scutellum of the grass embryo is a lateral organ, the equivalent of the foliage leaf. The epiblast represents the cotyledon that was lost in the evolution from the monocotyledonous condition, and the coleoptile is the third leaf. Opposed to this is WORSDELL'S² contention that the cotyledon, which he considers terminal in origin, is the lamina, and the coleoptile is the ligule, of a single foliage leaf, whose sheath was present only in early stages of development. The epiblast is said to be the equivalent of the auricles of the foliage leaf. The principal evidences brought to the support of this view are the double

¹ COULTER, J. M., and LAND, W. J. G., The origin of monocotyledony. II. Monocotyledony in grasses. Ann. Mo. Bot. Gard. 2:175-183. 1915.

² WORSDELL, W. C., The morphology of the monocotyledonous embryo and that of the grass in particular. Ann. Botany 30:509-524. 1916.

nature of the vascular system of the coleoptile, the bifid character of the epiblast in some grasses, and the forked coleoptile found in a few seedlings of maize. As a background for these details is the idea that the monocotyledonous condition is the primitive one.

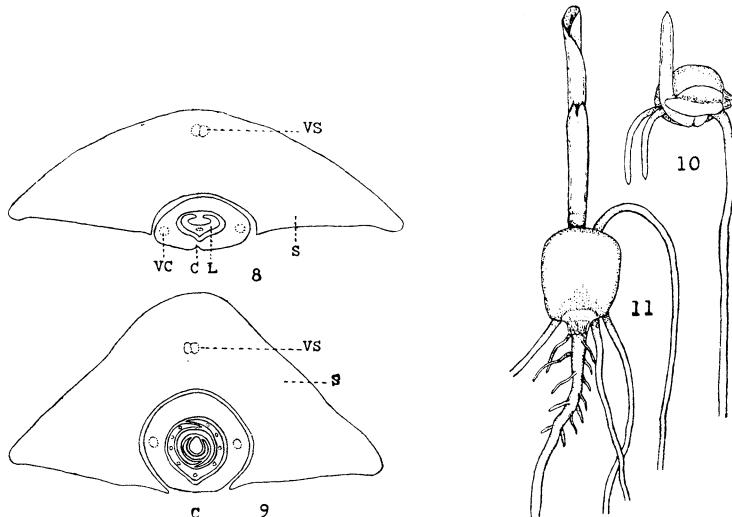
The first piece of evidence that I have to offer on these questions is in the form of a series of steps in the development of the embryo of maize (figs. 1-7). These stages have often been observed and



FIGS. 1-7.—FIGS. 1-6, steps in development of embryo: *C*, cotyledon; *S*, suspensor; *Co*, coleoptile; *L*, foliage leaf; *R*, root; *RS*, root sheath; $\times 15$; fig. 7, longitudinal section of nearly mature embryo: *S*, scutellum; *Co*, coleoptile; *L*, foliage leaf; *RC*, root cap; *RS*, root sheath; *Su*, suspensor; $\times 15$.

discussed more or less abstractly, but I have failed to find a complete series figured. In so far as appearances may be trusted, no evidence is clearer than this series. The appearance of the mature embryo (fig. 7) leaves little doubt of the terminal position of the plumule, and preceding stages of development bear this out fully; the cotyledon is never terminal, even in the earliest stages. As soon as the young embryo begins to differentiate, so that anything

that may be called a cotyledon is visible (fig. 1), the whole structure has an asymmetrical form due to the more rapid development laterally of the cotyledon, and subsequent steps emphasize this (figs. 2-7). That the coleoptile is at first directed horizontally or downward, as is emphasized by WORSDELL, is of little significance; morphological position cannot always be determined geometrically. Moreover, WORSDELL's³ figures, taken from another authority in



Figs. 8-11.—Figs. 8, 9, transverse sections of embryo through plumule: VS, vascular strands of scutellum; VC, vascular strands of coleoptile; L, foliage leaf; C, point of union between two sides of coleoptile, forming closed sheath; sections of embryo of liguleless variety in no essential way different from these; $\times 15$; fig. 10, germinating seed of liguleless maize: coleoptile present and normal; fig. 11, seedling of maize, showing forked coleoptile.

substantiation of his position, are only the upper parts of embryos; if we attach to the figures the lower parts of the corresponding stages of development of the embryo of any typical grass, the continuity of cotyledon, hypocotyl, and suspensor as the axis of the embryo is evident.

The second point in support of the view taken by COULTER and LAND is afforded by the embryo of a liguleless variety of maize isolated by EMERSON a few years ago. These plants are like those of ordinary maize, except that they breed true for the absence of

³ *Ibid.*, fig. 3, A-E, p. 511.

ligules and auricles. A few of the plants tend to produce at least rudimentary ligules on the uppermost leaves, but they are regularly absent from the lower leaves, and the condition might reasonably be expected to extend to the cotyledon also. An examination of the embryo and of the seedling, however, shows the coleoptile to be present and normally developed (figs. 8-10). While this fact cannot be accepted as a proof of anything, it should at least not be overlooked in considering the question.

WORSDELL has probably given undue emphasis to the arrangement of the vascular strands of the coleoptile and to the forked tip of this organ in some seedlings of maize (fig. 11). It is true that the coleoptile has two vascular strands bilaterally placed (figs. 8, 9), while the foliage leaf has several strands equally distributed; but this modification in vascular anatomy is no more significant than that shown in the scutellum (figs. 8, 9), in a prophyllum, or in the palea of many grasses, all of which tend to have their vascular elements present in two groups, and yet all of which are considered modified foliage leaves. The forked coleoptile is a common occurrence often noted by anyone having occasion to examine a large number of seedlings of maize, and it is due to a superficial set of conditions. The coleoptile begins to develop as an open sheath (figs. 2-4), the edges of which soon unite to form a closed structure; but the line of this union is always visible (figs. 8, 9), especially near the top of the sheath. Too much significance must not be attached to the nature of the mechanical rupture of this structure by the elongating plumule. If the union of the two sides has not been very firm, and it usually is not, the structure will split on one side only; but if the two sides are firmly grown together, the coleoptile may split for a short distance down two sides, producing the forked coleoptile (fig. 11). The relation between this occurrence and the duplex ligules of some grasses, or the two stipules of some other plants, is too remote to merit consideration.

It may be said, therefore, that the evidences derived from the structure and development of the maize embryo, including that of the liguleless mutant, favor the idea that the coleoptile is the homologue of a foliage leaf, and that the cotyledon is a lateral organ.